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The Leaf Thermotolerance of Nine Tree Species with Varying Geographic Range Sizes in a Climate Change-Threatened Hotspot

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Abstract: The Brazilian Atlantic Forest (*AF*) is recognized as one of the most threatened biodiversity hotspots by global climate change. Here, we examined the leaf traits (leaf mass area, leaf thickness, and chlorophyll content) and leaf thermotolerance (T_{50} and T_{Crit}) of seedlings of nine species of *AF* trees grown experimentally in order to foresee how extreme heat events will affect the forest's regeneration and diversity. Based on geographic range size, the species were classified into three groups, namely, species with a restricted-range distribution (endemic to the *AF*), species with an intermediate-range distribution (throughout the Brazilian tropical territory), and species with a wide-range distribution (Latin America). We found that the restricted-range group did not present lower thermotolerance compared to intermediate- and wide-range species groups. Surprisingly, leaf mass area had no effect on thermotolerance indices, while chlorophyll content and leaf thickness positively influenced T_{50} and T_{Crit}. Some species-specific responses to high-temperature stress deserve attention for tropical tree conservation, as is the case of *Arapatiella psylophylla*, a vulnerable endemic species with a very restricted-range distribution. Our results suggest that the species-specific leaf thermotolerance is an important criterion to be considered for tropical tree forest conservation in the context of global climate change.

Keywords: global warming; endemic species; heat stress; PSII chlorophyll fluorescence; tropical forest

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1. Introduction

The impact of global climate change on biodiversity is undoubtedly one of the greatest concerns of scientists, governments, and environmental managers in the 21st century. This phenomenon is closely related to the emission of greenhouse gases by human activities and has led to a gradual increase in average temperature worldwide [1,2]. Not only is the temperature rising, but the occurrence of extreme events such as heat waves and intense droughts has also become more frequent [3,4]. These events are predicted to increase in intensity and frequency in the coming years [2], which could affect the regeneration and establishment of seedlings of tree species in natural forest ecosystems and degraded restoration sites.

In particular, the impacts of climate change may be more intense in tropical forests, which have a more stable environment with less temperature variability than temperate and boreal zones [5,6]. In the tropics, the Atlantic Forest (hereafter *AF*) is one of the three hotspots in the world most threatened by global change, together with the Cape Floristic Province (South Africa) and the Polynesian and Micronesian islands [7]. Furthermore, the Brazilian *AF* is considered one of the most important biodiversity hotspots and hosts many endemic tree species [8]. The Central region of the Brazilian *AF*, which covers the south of the state of Bahia and the north of the state of Espírito Santo, has been considered a hot-point due to the high diversity of endemic and non-endemic plant species [9–12]. Currently, the AF is also under severe threat due to land-use changes and global climate change [9,11,13]. In this sense, a better understanding of how the increase in heat extremes will affect the diversity and endemic rates of the entire *AF*, including its central region, is fundamental for conservation.

Endemic species are generally more vulnerable to climate change than non-endemic species [14]. More than 60% of endemic tropical diversity is threatened with extinction in future climate scenarios [15]. This risk is usually associated with a small population size, habitat loss [16], a narrow range of distribution, and a small ecological niche [17]. Among the various factors influencing geographic range size variation (such as evolutionary time, dispersal potential, niche characteristics like tolerance to abiotic conditions), niche breadth has shown a strong relationship with range size [18]. Narrow niches tend to lead to smaller ranges and lower population size [18], a pattern often observed in endemic species. Consequently, a broader thermal niche is one of the most important aspects that may allow non-endemic species to occupy a larger geographic range than endemic species [19,20]. In particular, the ecological niche of endemic *AF* species is the Atlantic coastal area, which has a lower temperature variability and higher pluviosity than continental areas [21]. In this sense, endemic species, which have a restricted niche and restricted distribution near the coast, could be less thermotolerant than non-endemic species with a broader niche and range distribution. If this scenario is confirmed, the diversity of endemic species in the hot-point of the Central *AF* will decrease, with far-reaching consequences for the conservation of tropical ecosystems.

Studies that attempt to understand the limits of a species' thermal stress can help decipher species' vulnerability to temperature increases [22]. In this sense, the thermotolerance test has proven useful in identifying morphotypes and species that are more sensitive to heat stress [23,24]. Different approaches can be used for thermotolerance testing, such as visual damage, and changes in electrolyte loss, leaf gas exchange, and chlorophyll fluorescence [22]. In particular, the thermotolerance of chlorophyll *a* is one of the most commonly used techniques to assess the thermotolerance of wild and cultivated plant species, especially for ecological purposes [22,25]. This method is used to analyze how temperature affects the photochemical efficiency of photosystem II (*PSII*), which is the most heat-sensitive part of photosynthesis [26]. Although there are many studies on the thermotolerance of chlorophyll *a* that differ slightly in methodology, e.g., as the use of entire leaves, disks, or the timing of temperature heating, this technique is interesting because it is non-destructive, provides rapid results, and is relatively simple and inexpensive compared to other techniques [22]. The effect of heat stress on the photochemical efficiency of *PSII* can be measured using the F_v/F_m ratio to characterize the loss of photochemical efficiency as a function of temperature. This allows the calculation of thermotolerance traits such as T_{50} (the maximum temperature at which 50% of the initial F_v/F_m is lost) and T_{Crit} (the temperature at which F_v/F_m drastically decreases) and thus the comparison of different species, treatments, or individuals [27].

The present study was conducted with the aim of investigating the responses of nine *AF* species to extreme heat events. Considering that the ecological niche of *AF* geographically restricted endemic species is less variable and more restricted compared to wide-range non-endemic species, we hypothesize that endemic species have a lower thermotolerance than species with a broader geographic range distribution. We also assume that leaf traits are positively correlated with thermotolerance, particularly leaf mass area (*LMA*). Given these assumptions, we seek to answer the following questions: (i) Can Atlantic Forest tree species with different geographic range sizes cultivated under nursery conditions be distinguished in terms of their thermotolerance? (ii) Is there a relationship between thermotolerance and species leaf traits, such as *LMA*, leaf thickness, and chlorophyll content? (iii) Can leaf thermotolerance indices be used as a tool for conservation physiology? Using these questions, we examine the relationship between the thermotolerance, leaf traits, and range distribution of Atlantic Forest tree species.

2. Materials and Methods

2.1. Tree Species and Growth Conditions

In our study, we selected nine tropical tree species that are commonly used for forest restoration and silvicultural management [28,29]: *Arapatiella psilophylla* (Harms) Cowan, *Byrsonima stipulacea* hunb., *Cariniana legalis* (Mart.) Kuntze, *Cedrela odorata* Ruiz & Pav., *Copaifera lucens* Dwyer, *Eschweilera ovata* (Cambess.) Mart. ex Miers, *Gallesia integrifolia* (Spreng.) Harms, *Garcinia gardneriana* (Planch. & Triana) Zappi, and *Trema micrantha* (L.) Blume. All nine species occur spontaneously in the Central *AF*. The seeds came from different matrix sources all from the Central *AF* region and were acquired from the Arboretum Institute nursery in Teixeira de Freitas, Brazil (39°72′44″ W; 17°56′98″ S). The Central Atlantic Forest region has a hot and humid climate, classified as Af according to the Köppen system, without a pronounced dry season. Rainfall follows a gradient that decreases from the coast to the interior and from north to south. The annual rainfall is more than 1200 mm and reaches over 2000 mm in the wettest areas. The average annual temperature is between 22 °C and 25 °C [29]. In total, there are more than 150 rainy days per year in the region, with total precipitation exceeding 2000 mm per year [16]. All tree species have ecological and silvicultural importance and occur naturally in tropical and seasonal rainforests [30] and agroforestry systems associated with cocoa plantations in Brazil [29]. Also, three of the nine species in this study, *C. legalis*, *A. psilophylla*, and *C. odorata*, are vulnerable to extinction [31] (Tables 1 and S1).

Table 1. Distribution range, conservation status, and habitat of nine AF tree species used in this study.

Species	Distribution Range	Conservation Status	Habitat
Arapatiella psilophylla	Restricted	Vulnerable	Occurs mainly in primary forests with fertile, loamy, and well-drained soils
Byrsonima stipulacea	Wide range	Least Concern	Occurs mainly in poor, loamy soils, in primary or secondary forests
Cariniana legalis	Restricted	Vulnerable	Semi-deciduous forests in the lowlands; has a wide distribution from eastern to western South America, typical of regions with a pronounced dry season
Cedrela odorata	Wide range	Vulnerable	Grows in dry and humid habitats
Copaifera lucens	Restricted	Least Concern	Rainforests and semi-deciduous forests; primary and secondary formations and riparian forests; reduced radial growth associated with low rainfall
Eschweilera ovata	Intermediate	Least Concern	Degraded areas, forest gaps, and dry fragments, but grows better in moist forests

Table 1. *Cont.*

Species	Distribution Range	Conservation Status	Habitat
Gallesia integrifolia	Intermediate	Least Concern	Presents acclimation to increased shade and low water availability
Garcinia gardneriana	Wide range	Least Concern	Riverbanks and streams
Trema micrantha	Wide range	Least Concern	Occurs in all types of environments except very humid ones

Reference for distribution range, conservation [31] and habitat [32–38]. More information about the species is available on Table S1.

Based on the available literature [39], we categorized the tree species into three distribution range categories: restricted, intermediate, and wide. We defined restricted distribution as species endemic to the *AF* of southern Bahia and northern Espírito Santo (i.e., *A. psilophylla*, *C. legalis*, and *C. lucens*), whereas intermediate-range species are those restricted to the Brazilian territory and also found in other biomes and states (i.e., *E. ovata,* and *G. integrifolia*). Species distributed throughout Latin America (i.e., *B. stipulacea C. odorata*, *G. gardneriana*, and *T. micrantha*) were defined as wide-range species.

Ten seedlings per species were transferred to the nursery of Santa Cruz State University (UESC), located in the Central *AF* region in Ilhéus, Brazil (39°13′59″ W; 14°45′15″ S), and transplanted into 1.7 L pots containing forest soil. All plants grew under the same light, soil, and water conditions to avoid environmental bias when comparing the different species. The nursery had a light attenuation of 60% (around 20 mol photons m^{-2} day^{-1}), which is an intermediate light condition for all species. The seedlings were watered regularly. The lowest temperature recorded in the region during the growing period of the seedlings was 15.1 °C, while the highest temperature was 33 °C.

After four months, we estimated three leaf traits and started the photosynthetic thermotolerance test. On the day before the tests, the plants were irrigated abundantly and, at the beginning of the following morning, we selected one healthy, fully expanded, and mature leaf per plant for the evaluation of leaf traits and performance of thermotolerance tests.

2.2. Leaf Traits

For each tree seedling, we assessed leaf mass per area (*LMA*), leaf thickness (*LT*), and total chlorophyll content of a selected leaf (i.e., one leaf per individual, totaling 10 leaves per species). Chlorophyll concentration was measured with a SPAD-502 portable chlorophyll meter (Minolta, Japan) using the *SPAD* index, which was later converted to $\mu g\ cm^{-2}$ [40]. Leaf thickness (*LT*) was measured using an analogic micrometer (Zaas Precision, Brazil). Leaf or leaflet area (*LA*) was estimated using ImageJ 1.53e software [41,42] from photographs taken with a smartphone. The leaves and leaflets were placed on a standard white background sheet, which contained a scale used to calculate the *LA*. At the end of the thermotolerance essays, the leaves and leaflets were dried in a forced-air circulation oven at 60 °C until constant mass to obtain the dry mass (DM). The *LMA* was calculated through the formula $LMA = DM/LA$.

2.3. Test of Photosynthesis Thermotolerance

Immediately after the evaluation of leaf attributes, the chlorophyll fluorescence emission of each leaf was measured using a *Pocket PEA* portable fluorometer (Hansatech Instruments, King's Lynn, UK) to calculate the maximum quantum efficiency of photosystem II (F_v/F_m). This measurement corresponds to the initial F_v/F_m value at standard laboratory temperature (23 °C). To avoid the mechanical stress of cutting the leaf disks that resulted in water loss problems in previous tests (unpublished data), we used entire leaves or leaflets for all the thermotolerance tests. Entire leaves or leaflets have also been used previously for thermotolerance tests [21,43–45]. After measuring chlorophyll fluorescence, the leaves or leaflets were placed in sealed plastic bags to avoid water loss and direct contact with hot water. The bags were then immersed in a preheated water bath with a sous-vide system for slow cooking (Huispark, Zhihui Chen, China). In particular, the leaves or leaflets were exposed to six categories of temperature (i.e., 30, 35, 40, 45, 50, 55, and 60 °C) whose irreversible damage was already visually recognizable. The water temperature was measured using the multi-purpose thermometer *TM879* (Equitherm, Porto Alegre, Brazil) and no differences were found between the pre-programmed values on the sous-vide water heater and the reference thermometer. After 15 min at each temperature, the leaves or leaflets were placed between two layers of moist paper towels for a further 15 min in the dark at room temperature to measure $F_\mathrm{v}/F_\mathrm{m}$. Then, the leaves or leaflets were heated again at more 5 °C and the process was repeated up to 60 °C. The use of the same leaves occurred due to a limitation in the number of leaves available to the seedlings and to simulate the gradual increase in temperature [22]. The water temperature and $F_\mathrm{v}/F_\mathrm{m}$ data were used to determine the maximum temperature that promotes the loss of 50% of the initial $F_\mathrm{v}/F_\mathrm{m}$ (referred as T_{50}) and the temperature at which $F_\mathrm{v}/F_\mathrm{m}$ decreases dramatically (referred to as T_Crit) [6,44,46]. We used the equations described in [24] to estimate T_{50} and T_Crit using the formula of Equation (1):

$$F_v/F_m = (F_v/F_{m,Max})/(1 + e^{b\cdot(T_{leaf} - T_{50})}) \tag{1}$$

where $F_\mathrm{v}/F_\mathrm{mMax}$ is the upper horizontal asymptote representing $F_\mathrm{v}/F_\mathrm{m}$ associated with healthy, non-stressed leaves; b is the steepness of the decrease in $F_\mathrm{v}/F_\mathrm{m}$ around T_{50}; and T_Leaf is the incubation temperature (°C) of the leaf. During the thermotolerance tests, the temperature of the laboratory's air conditioning was set at 23 °C.

2.4. Statistical Analysis

The thermotolerance curves were fitted with the "*nlsLM*" function from the minpack.lm package in R version 4.2.1 [47]. From the curves, we estimated the individual values of T_{50} and $F_\mathrm{v}/F_\mathrm{mMax}$ for each plant individual and calculated the mean species' values with their standard errors. T_Crit was estimated as the temperature at which a line describing the slope of the $F_\mathrm{v}/F_\mathrm{m}$ decline at T_{50} intersected with a horizontal line indicating $F_\mathrm{v}/F_\mathrm{mMax}$ (data available in Table S4) [24]. For a better fit of the models by species, we excluded the curves from individuals (plants) deemed outliers (i.e., $R^2 < 0.60$). Consequently, we removed the complete dataset of one individual each from *A. psilophylla*, *C. legalis*, *C. odorata*, *E. ovata*, and *G. gardneriana.* Likewise, in *C. lucens*, we excluded individuals with low initial $F_\mathrm{v}/F_\mathrm{m}$ values at 22 °C leaf disk heating (i.e., $F_\mathrm{v}/F_\mathrm{mMax} < 0.650$), leaving only three individuals for this species (data available in Table S5). Curves were compared using maximum likelihood for the best fit and were selected according to the lowest Akaike information criterion corrected (AIC_c) for small samples [48].

The thermotolerance parameters (T_{50} and T_Crit) and the leaf trait variables (*LMA*, *LT*, and total chlorophyll content) were compared between the species using Fisher's one-way ANOVA or the Kruskal–Wallis test with post hoc Tukey's Honest Significant Difference test or Bonferroni's test (respectively) in order to describe and compare the species thermotolerance.

Using generalized linear mixed models, we assessed the effects of leaf traits (*LMA*, *LT*, or chlorophyll content) on thermotolerance indexes (T_{50} or T_Crit), including the distribution range categories (restricted, intermediate, and wide) as fixed effects. To account for the species effect, we also used the species as the random effect in the model. The Tweedie family distribution was selected for the model according to the test of singularity, convergence, zero inflation, and overdispersion. The model showed convergence but no singularity. All statistical analyses were performed using R statistical software with the *glmmTMB* function from the *glmmTMB* package [49].

In order to test whether the species thermotolerance differed along different range groups, we compared the values to T_{50} and T_{Crit} among the three distribution range categories (i.e., restricted, intermediate, and wide) using the Kruskal–Wallis test. All statistical analysis were performed in R version 4.2.1.

3. Results

3.1. Thermal Tolerance in AF Species

The nine tropical tree species exhibited an initial maximum photosystem efficiency $F_{\mathrm{v}}/F_{\mathrm{m}}$ varying between 0.7 and 0.8, implying no photodamage or other stress (Figure 1). In particular, high $F_{\mathrm{v}}/F_{\mathrm{m}}$ values were maintained at a room temperature of 23 °C up to 30 °C for most species. However, a sharp decline was observed above 40 °C to 50 °C in all species, with the T_{Crit} ranging from 45 °C to 51 °C. In our study, we also detected that the T_{50} ranged from 49 °C to 54 °C. Only *G. gardneriana* maintained an $F_{\mathrm{v}}/F_{\mathrm{m}}$ above 0.2 at 60 °C, while most tree species reached an $F_{\mathrm{v}}/F_{\mathrm{m}}$ value equal to zero at this temperature (Figure 1). Among the studied tree species, *G. gardneriana* and *G. integrifolia* achieved the highest mean values of T_{50} (Figure 2), with, respectively, 54.84 °C and 54.59 °C. The lowest mean values of T_{50} were observed in *A. psilophylla*, *E. ovata*, *C. odorata*, and *T. micrantha*, ranging between 49.50 °C and 50.71 °C. The other three species, *B. stipulacea*, *C. legalis*, and *C. lucens*, remained in between those extremes.

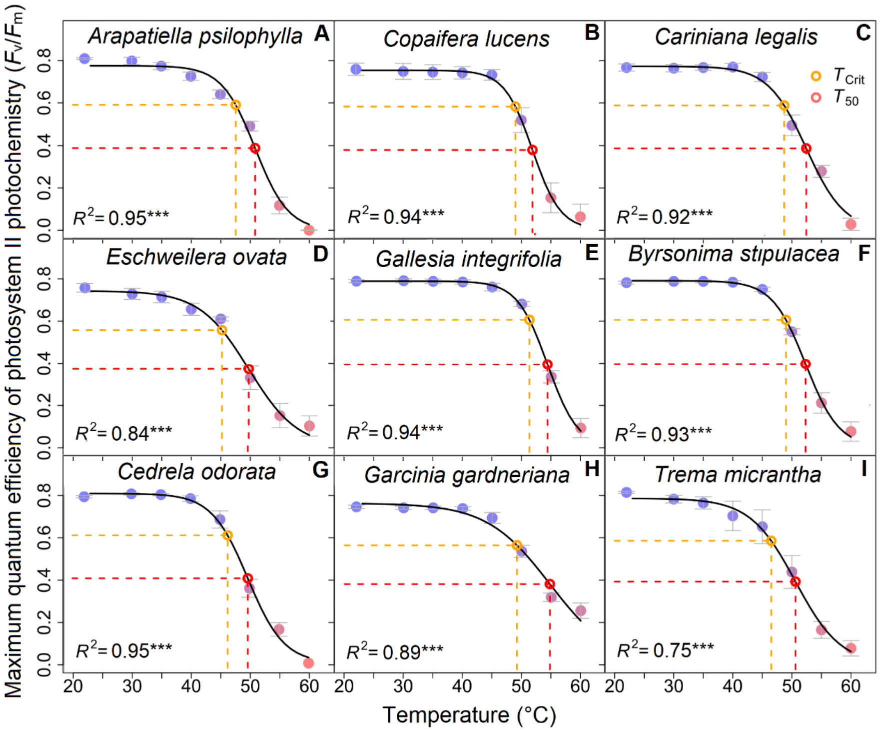

Figure 1. Thermotolerance curves of nine tropical tree species with different geographical range sizes. Species with (**A**–**C**) restricted geographic range (endemic AF species), (**D**,**E**) intermediate geographic range (occurring along the Brazilian territory), and (**F**–**I**) wide geographic range distributions (occurring throughout Latin America). The red dashed lines represent the T_{50} and the orange dashed lines indicate T_{Crit} ($p > 0.001$ represented ***).

Among the species analyzed, *G. integrifolia* and *B. stipulacea* had the highest T_{Crit} values, at 50.89 °C and 49.42 °C, respectively. *G. gardneriana*, *C. legalis*, and *C. lucens* reached middle values (around 53 °C), while *A. psilophylla*, *E. ovata*, *C. odorata*, and *T. micrantha* presented the lowest values ranging between 45.54 °C and 47.38 °C (Figure 2 and Table S2).

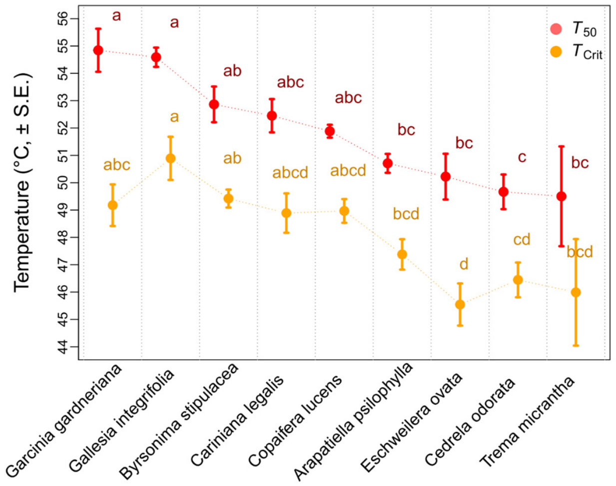

Figure 2. T_{50} and T_{crit} of nine tropical tree species. Different letters indicate significant difference ($p \leq 0.05$) among species. Values are represented by mean and standard error of temperature.

3.2. Leaf Traits and Thermotolerance

Regarding the leaf traits, we observed that the mean *LMA* values ranged from 40 to 160 g m^{-2}, *LT* ranged from 0.15 to 0.35 mm, and the plants' chlorophyll content ranged from 28 to 61 µg cm^{-2} (Figure 2). Chlorophyll content was not related to species range distribution. According to the Kruskal–Wallis test, the lowest and highest values of leaf mass area and chlorophyll content were recorded in the wide-range species *C. odorata* and *G. gardneriana*, respectively (Figure 3).

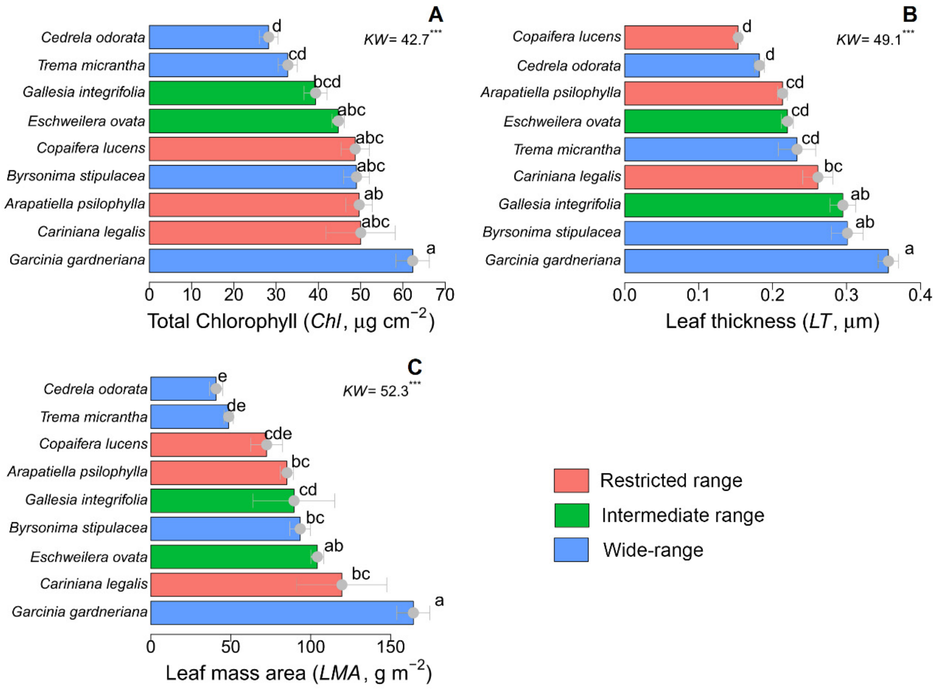

Figure 3. Leaf traits of nine tropical tree species grouped into three range distribution categories: restricted range (endemic AF species), medium intermediate range (occurring along the Brazilian territory), and wide distribution range (occurring throughout Latin America). (**A**) Total chlorophyll content, (**B**) leaf thickness, and (**C**) leaf mass area. Different letters indicate significant differences among species (*** represents $p > 0.001$; values: mean ± standard error).

Regarding the relationship between the leaf traits and thermotolerance, chlorophyll content positively influenced T_{50}. The same was found for leaf thickness in T_{Crit} (Figure 4; Table S3).

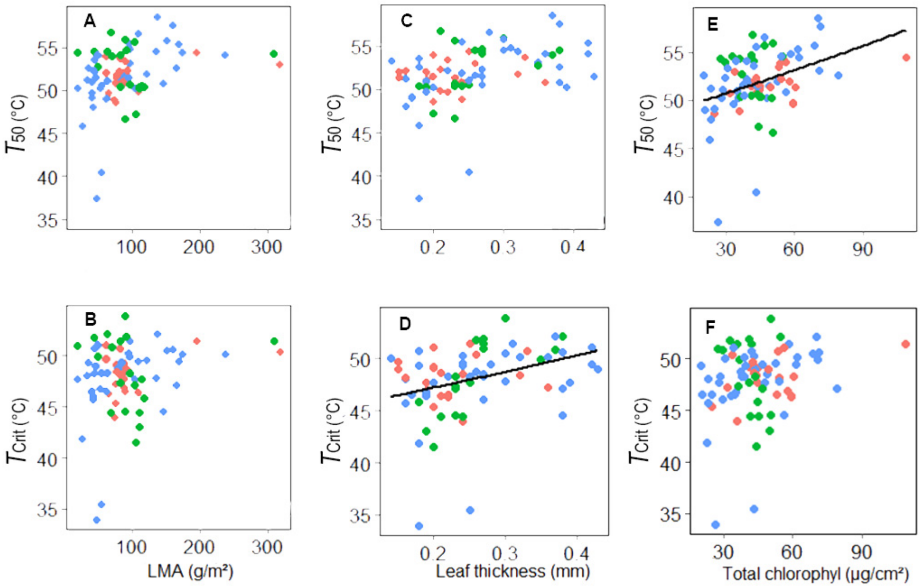

Figure 4. Relationship between thermotolerance indexes T_{50} (**A**,**C**,**E**) or T_{Crit} (**B**,**D**,**F**) of nine tropical tree species and their leaf traits: leaf mass area—*LMA* (**A**,**B**); leaf thickness (**C**,**D**); and chlorophyll content (**E**,**F**). Red, green, and blue represent, respectively, restricted-, intermediate-, and wide-range species. The black line represents the fitted regression line of the generalized linear mixed model.

3.3. Species Range Distribution and Tolerance

Species with a wide distribution had T_{Crit} values of around 49 to 45 °C and 49 to 54 °C of T_{50}. For intermediate-range species, T_{Crit} was 45 to 50 °C and T_{50} was 50 to 54 °C. Restricted-range species presented T_{50} values of 45 to 50 and T_{Crit} of 50 to 52 °C. Our findings indicated no significant differences in T_{50} and T_{Crit} among the three distribution range categories (Figure 5).

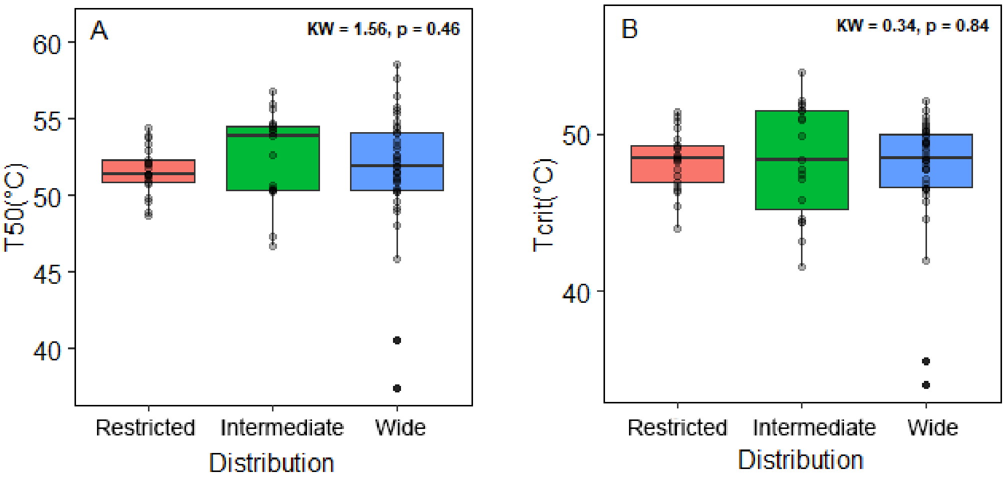

Figure 5. Thermotolerance indexes of the tree tropical species grouped in three distribution range categories: restricted range (red), intermediate range (green), and wide range (blue). (**A**) T_{50} indicates the temperature that promotes the loss of 50% of the initial F_v/F_m, and (**B**) T_{Crit} represents the temperature at which F_v/F_m decreases dramatically. In the upper right corner, we indicate the values of the Kruskal–Wallis test and the significance.

4. Discussion

Our study aimed to answer how nine species of the Central *AF* will respond to extreme heat events according to their geographic range size and leaf traits. We expected geographically restricted *AF* species (endemic to *AF*) to show less variability in leaf traits and thermotolerance than intermediate- and wide-range (non-endemic) species due to their restricted ecological niche. A similar hypothesis has been tested before, but no consensus has yet been found. For example, in bromeliads, the endemic species *Vriesea minarum* did not exhibit a lower thermotolerance than the two widespread bromeliad species, *Vriesea bituminousa* and *Aechmea nudicaulis* [45]. In tropical trees, there is some evidence of a positive relationship between the maximum leaf temperature across different geographic distributions and thermotolerance (T_{50}) [6]. A negative relationship was also observed between habitat elevation, a factor associated with species distribution, and thermotolerance [27]. In our study, we compared endemic plant species of the Central region of *AF*, characterized by a restricted-range distribution and stable habitat (low temperature variability), with other species with a wide-range distribution, found throughout Latin America, and found no significant difference in thermotolerance. Thus, our results suggested that thermotolerance is not directly related to species geographic range size, and the hypothesis that endemic species with restricted ranges have a lower thermotolerance than species with wider range sizes was refuted. In this sense, species geographic range size likely has little influence on the thermotolerance of trees in the habitats and species studied.

The fact that no lower thermotolerance was found in the restricted-range species group suggests that the range size restriction for these species is not driven by thermal tolerance, and may be related to other abiotic factors (such as soil) or biotic factors (such as dispersion or competition) [50]. *Arapatiella psilophylla*, *Eschweilera ovata*, *Cedrela odorata,* and *Trema micrantha* are among the least thermotolerant species, indicating a high vulnerability to future extreme heat events. Specifically, *A. psilophylla* is on the IUCN Red List of Threatened Species [51] and is endemic to the Central *AF* region. This species is recommended in forest restoration because it attracts general fauna and increases soil nutrient content [52]. The small population, limited niche, and barochorous dispersal contribute to the classification of this restricted-distribution species as vulnerable to extinction (IUCN Vulnerable category) [53]. Further concerns arise from the low thermotolerance observed in this species, which emphasizes the need for measures to protect it [52]. Another iconic species is *C. odorata*, which is also a threatened species, but with anemochory dispersion and a wide-range distribution through Latin America [54]. Although *C. odorata* is more thermotolerant than *A. psilophylla*, its conservation remains critical given its role as a keystone species. This tree is an emergent species with a large canopy that plays a key role in maintaining biodiversity by providing shelter, food, shade, moisture, and other resources to other species [51]. Thus, among the nine species studied, these two stand out for their higher risk of extinction, which could be aggravated by climate change, emphasizing how fragile the diversity of the *AF* can be.

We could not detect any effects of *LMA* on thermotolerance indices, but we found that chlorophyll content and leaf thickness positively affected T_{50} and T_{Crit}. Functional traits such as seed weight, *LMA*, wood density, and tree height are used to reveal ecological differences among tropical tree species [5]. In particular, *LMA* is an important, widely used leaf trait in the context of ecology and the regional distribution of plant species [55]. Higher *LMA* is generally associated with less favorable environmental conditions, as seen in sclerophyllous and xeromorphic plants in warm or dry environments [55,56]. In this sense, we expected *LMA* to be positively related to thermotolerance, as observed in some previous studies [27,57]. However, there was no significant correlation between thermotolerance (T_{50} and T_{crit}) and *LMA*.

Differences in leaf traits among species could also be related to ecophysiological strategies associated with the survival and growth of tree seedlings in the forest understory [58,59] or defense against herbivory [60], rather than species-specific thermotolerance [61]. In this sense, *Garcinia gardneriana* had the highest values for *LMA*, *LT*, and chlorophyll content among the species studied and was among the species showing the highest thermotolerance indices, being the only species that did not reach 0 F_v/F_m at 60 °C. The species in question occupies a wide ecological niche, growing in ecosystems with different temperatures and water availability, such as the Amazon, the Caatinga, the Cerrado, and the Atlantic Forest [39]. Thus, although there is no relationship between leaf traits and thermotolerance, they could contribute to the establishment of the plant in different environments, especially for *G. gardneriana*.

Tropical species generally have a photosynthetic thermal optimum around 30 °C and a further decline at 40 °C and 50 °C, corresponding to T_{Crit} [46,57,62,63]. Similar results were also found in the nine species studied in this experiment. The critical temperature threshold of 40–50 °C is only a few degrees above the temperature experienced by leaves in the upper canopy of tropical trees, which exceed 40 °C at midday [63,64]. With the increasing frequency and intensity of extreme events, such temperatures will be reached and exceeded more frequently [65,66]. These changes will affect populations, and it is important to take action to protect the most vulnerable species [67].

Thermotolerance tests using chlorophyll fluorescence have proven to be a useful tool for determining the limits of a species' heat stress and deciphering species' vulnerability to temperature increases, which can aid in conservation efforts [22]. It is important to emphasize that all tested seedlings originate from the Central *AF*, the only place where all species occur together. The genotype of the populations could be adapted to the local environmental conditions and possibly influence their thermotolerance. To our knowledge, there are only a few studies looking at the differences in thermotolerance between different genotypes [68], but there is no study with T_{50} and T_{crit}. However, recent studies suggest that thermotolerance, although it may vary depending on the site of origin [69], has a lower plasticity compared to other leaf traits [45,57,70]. Therefore, the thermotolerance indices, especially the T_{50}, could help improve the criteria for classifying species according to their extinction risk due to climate change in the context of conservation physiology [71,72]. Conservation physiology is a scientific discipline that aims to solve conservation problems using physiological concepts and tools [71]. In this sense, T_{50} could be a particularly interesting tool to determine which species should be prioritized for conservation efforts and management planning in a broader framework of in situ and ex situ conservation efforts [72]. It is also recommended that conservation institutions preserve genetic material from multiple populations of these species for germplasm banks, seedlings for botanical gardens, and seeds for seed banks and thus partially perpetuate the variability in the species.

5. Conclusions

Our study suggests that there is unlikely to be a displacement of *AF* endemic species by non-endemic species due to future heat waves. We found no difference in the T_{50} and T_{Crit} of species with different range sizes, showing that the restriction of the occurrence of endemic species is not driven by thermotolerance. T_{50} has a greater potential to improve the criteria for classifying species according to their extinction risk in future climate scenarios compared to T_{Crit}. This study contributes to the development of theoretical approaches and conservation practices related to species composition. This is especially important since tree diversity is one of the most vulnerable hotspots due to global climate change.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f16050764/s1, References [73–77] are cited in the supplementary materials. Table S1: Botanical family, geographical range, conservation status and other aspects of nine tropical tree species used in our study. Table S2: Distribution range, thermotolerance and leaf traits values of nine tropical tree species. Table S3: Results of the generalized linear mixed models used to assess the influence leaf traits and distribution range categories on thermotolerance indexes. Table S4: Leaf traits and fluorescence parameters over temperature increasing from nine forest species studied. Table S5: Model results for the determination the response of Fv/Fm over temperature increasing for nine forest species studied.

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